that could not be included in the cladistic analysis, because of the absence of anatomical information. In this classification, the Conoidea comprises the six families Drilliidae, Terebridae, Pseudomelatomidae, Strictispiridae, Turridae, and Conidae. Five of these are monophyletic according to the cladogram, but Turridae is both diphyletic and paraphyletic.

These problems are not readily resolvable, and the classification of the Conoidea remains in a state of flux. As next steps toward more satisfactory solutions we suggest exploring classifications based more closely on the results of Taylor, Kantor, and Sysoev's cladistic analysis than is their proposal, and enhancing their analysis by incorporating additional characters.

Alan J. Kohn
James H. McLean

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Reply by Dr. Taylor

We welcome the interest in our paper; the Conoidea are a fascinating group of gastropods and despite the disproportionate attention devoted to the shells of some of the taxa, our knowledge of relationships within the superfamily is very poor. We are very aware of the many inadequacies in our study, principally deriving from the fact that the Conoidea are such a diverse group, so that the species which have been studied anatomically represent only a small subsample of the total diversity. Primarily, we attempted to demonstrate that there are many features of the conoidean foregut which can be utilized in phylogenetic analysis. This information was obtained from serial sections of the proboscis and foregut of about 70 species of conoideans, integrated with information from previously published studies. Other organ complexes such as the reproductive system will likely yield further suites of characters but, as yet, remain uninvestigated.

Kohn & McLean advocate using more shell characters and fossil taxa in future analyses. However, we fail to see how the inclusion of fossils would corroborate the phylogeny as they suggest. Our work on turrids and terebrids has shown that shell characters are often a poor guide to internal anatomy. Recent studies of species of the subfamily Crassispirinae have highlighted the fact that animals with rather similar shells e.g., *Ptychobela, Funa,* and *Inquisitor* possess very different radulae and foregut anatomies (Kilburn, 1988, 1989; Taylor, in press). Additionally, some species placed in the Mangeliinae on the basis of shell characters turn out to have crassispirine anatomy (Kilburn & Taylor, unpublished). The problem is particularly acute in the Terebridae, where shells can be extremely similar but reveal quite different foregut structures e.g., *Terebra subulata* has a proboscis, hypodermic radula, venon gland, and accessory salivary glands, whereas *Terebra areolata* lacks all these structures. By contrast, a wide range of shell form is found within the Daphnellinae, but species share many common anatomical characters.

The authors highlight the fact that the classification we propose is not a direct transposition from the cladogram. We are of course conscious of the problems of developing a formal classification from the cladogram and very aware that some of the taxa we propose may be paraphyletic. As we were careful to point out (p. 157), the classification we propose represents a conservative compromise, and there are several reasons for this restraint. Primarily, the number of species we analyzed in the cladogram is only a small subset of the total diversity of conoideans, and new combinations of foregut structures are still being discovered (Kantor & Taylor, 1994; Taylor, in press). Moreover, the cladogram was not particularly well resolved or robust, and some nodes are supported by rather few, possibly weak characters. New and continuing work should help resolve some of these problems, although Arnold (1990) has suggested reasons why morphological phylogenies of some groups may never be well resolved.

Perhaps the feature of the classification which has vexed Kohn & McLean the most is the "downgraded" status of Coniinae. The *Conus* species that we have studied have a relatively underived foregut anatomy (compared to, say, the Mangeliinae and Daphnellinae), which is very similar to that of species in the "borsoniine" group of our Clathurellinae. They have a buccal mass situated at the base of the proboscis, a single accessory salivary gland, acinous salivary glands, and a radular caecum. The venom gland is unchanged in histology anterior to the nerve ring, and the buccal lips are unmodified. The proboscis sphincter lies in an intermediate position within the buccal tube, but

this probably represents a posteriorward shift of the anterior sphincter to accommodate the long radular teeth of *Conus*. The snout gland, situated in the posterior of the rhynchodeum, may turn out to be an autapomorphy of *Conus*, but its distribution is unknown in conoideans other than those we have studied. As Kohn & McLean point out, internal shell resorption has in the past been used as a character to define the Conidae. We considered, but did not include this character in the cladistic analysis. Its inclusion would have made no difference to the structure of the cladogram except to add another apomorphy at the node of *Benthofascis* and *Conus*. Internal remodelling of the shell, involving both dissolution and deposition, is seen to a degree in many gastropods, and it is likely that *Conus* represents one extreme of this phenomenon.

John D. Taylor

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